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Fluctuating Asymmetry and Morphometric Variation of Hand Bones

GREGORY LIVSHITS,* KONSTANTIN YAKOVENKO,
LILIA KLETSELMAN, DAVID KARASIK,
AND EUGENE KOBYLIANSKY
Research Unit–Human Population Biology, Department of Anatomy and Anthropology, Sackler Faculty of Medicine, Tel Aviv University, Ramat Aviv 69978 Israel

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ABSTRACT The major aim of this study was to test three hypotheses: 1) more complex traits of the hand are less prone to developmental insults and therefore show lower fluctuating asymmetry (FA) as compared with simple traits; 2) the manifestation of FA correlates with the variability of the trait (i.e., CV); and 3) FA is an organ-wide property, and therefore a concordance exists between the FA measures of different traits in hand bones. Seventy-two bilateral measurements of hand bones, were made from plain-film radiographs of 365 cadavers. A complex trait was considered as the total length of the three phalanges of a finger and their contiguous metacarpals. Simple traits were considered to be the lengths of individual bone that made up the complex trait. The following results were obtained: 1) on the average simple traits, composing the complex trait, show much higher FA than the corresponding complex trait, but this result is expected if there is no correlation (or low correlation) between FA of simple traits within the complex trait, due to random direction of right-left differences; 2) strong and highly significant correlation was observed between FA and CV of studied traits, regardless of sex and age of individuals; and 3) the majority of FA measurements of hand bones showed no correlation. However, correlations between some sets of FA traits were highly significant. They were interpreted, although not specifically tested, as the result of a tight relationship between traits related not only developmentally but also by active performance of the same function. Am J Phys Anthropol 107:125–136, 1998.

There are many published data that indicate the relationship between developmental homeostasis as assessed by fluctuating asymmetry (FA) and human health status (reviewed in Livshits and Kobyliansky, 1991; Fraser, 1994; Moller, 1996; Thornhill and Moller, 1997; see also, e.g., Mellor, 1992; Kieser and Groeneveld, 1994; Goldberg et al., 1995; Naugler and Ludman, 1996a; Kieser et al., 1997; Kobyliansky et al., 1997a). However, the results of numerous other studies are often contradictory (e.g., see array of papers edited by Markow, 1994), and theoretical considerations of FA origin still raise a variety of opinions (Clarke, 1995; Naugler and Ludman, 1996b; Moller and Swaddle, 1997).

One of the potential sources of FA may be the biological nature of the bilateral trait itself. Thus, Soule (1982) suggested that morphological traits of greater complexity

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*Correspondence to: Gregory Livshits, Research Unit–Human Population Biology, Department of Anatomy and Anthropology, Sackler Faculty of Medicine, Tel Aviv University, Ramat Aviv 69978, Tel Aviv, Israel. E-mail: gregl@ccsg.tau.ac.il

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should be less prone to random environmental effects and therefore should possess a higher developmental stability (i.e., lower FA). Such traits should also have a lower coefficient of variation (CV) due to a strong involvement of genetic factors in their variation. Soule (1982) therefore proposed "the more components in a system or structure, the lower should be the CV." The corollary of this hypothesis is the existence of a strong positive correlation between the CV and FA of the trait.

Soule's (1982) hypotheses can be tested by comparing the phenotypically extreme individuals vs. modal phenotypes using, for example, estimates of FA and CV for the different parts of a distribution of the same trait (Soule and Cuzin-Roudy, 1982; Clarke, 1995). The other way of testing is by comparing FA of the given trait *X* in individuals sampled from the different parts of the distribution (extremes vs. center) of trait *Y* (Kobyliansky and Livshits, 1986; Livshits and Kobyliansky, 1987; Livshits and Smouse, 1993).

Conversely, there are practically no studies where different traits, functionally related one to the other and having substantially different CV, were compared with respect to FA. That is, we assume here that, within the same species, morphological traits that differ in developmental stability will differ in the extent of CV and FA in the same direction (i.e., significant positive correlation between the CV and FA is expected). Together with this, homologous traits which differ in complexity will show a different magnitude of FA, which will negatively correlate with the degree of complexity. Moreover, because the testing of these two assumptions requires a large number of bilateral variables, the integration of FA measures can also be tested.

Since FA reflects the developmental stability of an individual or its breakdown due to genetic or environmental sources, whether FA is an organism-wide property was repeatedly tested (Thoday, 1958; Livshits and Kobyliansky, 1985; Livshits et al., 1988; Parsons, 1990; Leamy, 1994; Watson and Thornhill, 1994; Brakefield and Breuker, 1996; Dufour and Weatherhead, 1996). Soule and Cuzin-Roudy (1982, p. 766) assumed, however, that "within individuals, asymmetries are uncorrelated" and that FA represents "a measure of character specific stability in a population." Indeed, the results of the above mentioned studies are very different, and various arguments were invoked to explain this disconcordance (e.g., Dufour and Weatherhead, 1996).

In the present study, we use a large number of individuals and bilateral traits of the hand bones, to test three hypotheses: 1) more complex traits are less prone to developmental insults and therefore show lower FA as compared with simple traits; 2) the manifestation of FA correlates with the variability of the trait (i.e., CV); and 3) FA is an organ-wide property, and therefore a concordance exists between the FA measures of different traits.

MATERIAL AND METHODS

Sample and measurements

The sample includes a total of 365 subjects, aged 17–96 years and comprises 206 males and 159 females, corpses of the L. Greenberg Institute of Forensic Medicine, Tel Aviv, Israel. The collecting of the sample was carried out over a period of 2 years (1993–1994). The mean age for males is 45.6 years (17–95 years old) and for females 56.5 years (17–96 years old).

Both hands of all subjects were subjected to X-ray filming (the detailed description of the method and the sample is given by Kobyliansky et al. [1995, 1997b]). Radiographs of the hand were taken in the posteroanterior position with the X-ray source 60 cm above. These were exposed for 5–10 s at 100–150 mA without intensifying screens at 50 kV. Only hand bones of the second to fifth fingers were examined; those of the first finger do not project directly in roentgenography and therefore were not studied. The measurements comprised bone dimensions on radiographs, including the length and width of each bone of the hand, excluding the first metacarpal and first finger bones, as accepted in anthropology (Plato and Norris, 1980; Kobyliansky et al., 1985). Cortical and medullary diameters of the metacarpals were measured using a technique recommended by Garn et al. (1976) and Dequeker (1976). The measurements were carried out on plain-film radiographs of each of the four metacarpal bones (second to fifth) as well as

Fig. 1. The list of variables used in the study and their abbreviations[1]

Bone	Measurement: Length (1)[1]	Width of bone in midshaft (2)[1]	Width of medular canal in midshaft (3)[1]	Width of proximal epiphysis (4)[1]	Width of distal epiphysis (5)[1]
Metacarpal[2]	L3MLEN;	L3MWID;	L3MCAN;	—	L3MDWIDE;
	R3MLEN;	R3MWID;	R3MCAN;	—	R3MDWIDE;
Proximal phalanx	L3PLEN;	L3PWID;	L3MCAN;	L3PPWIDE;	L3PDWIDE;
	R3PLEN;	R3PWID;	R3MCAN;	R3PPWIDE;	R3MDWIDE;
Middle phalanx	L3SLEN;	L3SWID;	L3MCAN;	L3SPWIDE;	L3SDWIDE;
	R3SLEN;	R3SWID;	R3MCAN;	R3SPWIDE;	R3MDWIDE;
Distal phalanx	L3DLEN;	L3DWID;	—	L3DBAS (6);[1,3];	L3DTUB (7);[1,4]
	R3DLEN;	R3DWID;	—	R3DBAS (6)[1]	R3DTUB (7)[1]
Length of ray (8)[1]	R3RAY = R3MLEN + R3PLEN + R3SLEN + R3DLEN				
	L3RAY = L3MLEN + L3PLEN + L3SLEN + L3DLEN				

[1]Numbers in parentheses are related to the measurements indicated in Fig. 1. Measurements were performed on metacarpals and phalanges of the second to fourth finger on the left (L) and right (R) hands. Number 3 indicates the third finger, as an example.
[2]Measure.
[3]Width of base of distal phalanx.
[4]Width of tuberosity of distal phalanx.

of each of the four proximal and middle phalanges (second to fifth) by one of the authors using a digital caliper connected to an IBM PC. The measurements are shown in Figure 1. Each individual in the present study was assessed for the same 72 osteometric traits for right and left hands separately. The list of traits and their abbreviations is given in the legend to Figure 1.

Statistical analysis

Measurement of fluctuating asymmetry (FA). Following Palmer's (1994) recommendations, we used two measures of FA

(FA2 and FA6, according to Palmer's definition). These are the most frequently used measures that also allowed us to compare our results with those recently published (e.g., Leamy, 1994; Dufour and Weatherhead, 1996). FA2 is adjusted for the size of the trait, the absolute difference between the right (Rt) and left (Lt) side measurements of the trait. In the present study, Rt-Lt differences of the studied bilateral traits showed correlation with trait measurements. To remove this size dependence of Rt-Lt, we divided the difference by the mean size of the Lt and Rt sides of the trait for the individual—that is, $FA2 = 2|Rt\text{-}Lt|/(Rt + Lt)$. $FA6$ is a variance of Rt-Lt differences for each trait—that is, $FA6 = \Sigma(dS_i - DS)^2/n - 1$, where $dS_i = 2(Rt_i - Lt_i)/(Rt_i + Lt_i)$, $DS = 1/n\ \Sigma dS_i$, and n is the sample size.

The FA measurement can be inflated by the presence of antisymmetry (AS) and directional asymmetry (DA). To test for the presence of AS and DA, we tested the distribution of Rt-Lt difference for each trait for normality and significance of skewness and kurtosis. Taking into account Bonferroni's correction for multiple comparison (Sokal and Rohlf, 1987; Rice, 1989), the studied traits showed no significant platykurtotic distributions (Fig. 2). However, the existence of DA was possible due to significant skewness in some trait distributions (Fig. 2). To correct for DA, we substracted the mean of the Rt-Lt difference from each individual difference (for details see Livshits et al., 1988).

Measurement error. To examine the degree of measurement error as compared with the magnitude of FA, we measured the first 30 individuals twice, with substantial time intervals between the first and second measurement. We used Fields et al.'s (1995) approach to calculate the reliability coefficient of FA for each trait. The reliability coefficient (REL) is the proportion of variance (V) free of intraobserver measurement error. It corresponds to the interclass correlation coefficient and is given by

$$REL = \frac{V\{0.5[(Rt_1 + Rt_2) - (Lt_1 + Lt_2)]\}}{V\{0.5[(Rt_1 - Lt_2) + (Rt_2 - Lt_2]\} + V[(Rt_1 - Rt_2) - (Lt_1 - Lt_2)]}.$$

With just a few exceptions, the magnitude of a measurement error, $ME = 0.5\{|Rt_1 - Rt_2| + |Lt_1 - Lt_2|\}$ was much smaller than $FA = |Rt - Lt|$. We note that the ratio FA2/ME was within the range of 2.5–8 for about 90% of the traits. There was no clear association between the average FA level of the trait and corresponding ME ($r = -0.21$, $P > 0.05$). Because of this situation, we did not exclude from consideration traits with relatively low reliability of FA and assumed that ME is distributed randomly around particular FA measurement.

Comparison of traits. One of the major aims of this study is to compare the FA of complex traits with the FA of simple traits. To make complex and simple traits comparable, we defined for this part of the study the total length of four hand bones (i.e., the three phalanges of a finger and contigious metacarpal [RAY]) as a complex trait and defined the length of each bone composing the corresponding ray as a simple trait. Each ray thus contains the following four bones: metacarpal, proximal, middle, and distal phalanges (Fig. 1).

For each complex and simple trait, both FA2 and FA6 were computed. Paired comparisons of the fluctuating asymmetry (RAY-FA) of each ray with the respective four bones were carried out. Because the FA2 distribution strongly violates the assumption of normal distribution (e.g., Livshits et al., 1988; Palmer, 1994), FA2 measures were compared by nonparametric Kruskal-Wallis analysis of variance (ANOVA) tests. FA6 measures were compared by parametric ANOVA tests.

To study the relationship between the extent of FA and variation of trait, we computed the coefficient of variation (CV) for each trait. The correlation between CV and FA2 was then investigated by sex and age cohort.

Integration of FA measurements. To study the extent to which FA measurements of different hand bone traits correspond one to another, we computed two types of pairwise correlations between individual FA2ij measurements: the Pearson product moment correlation and the Nonparametric

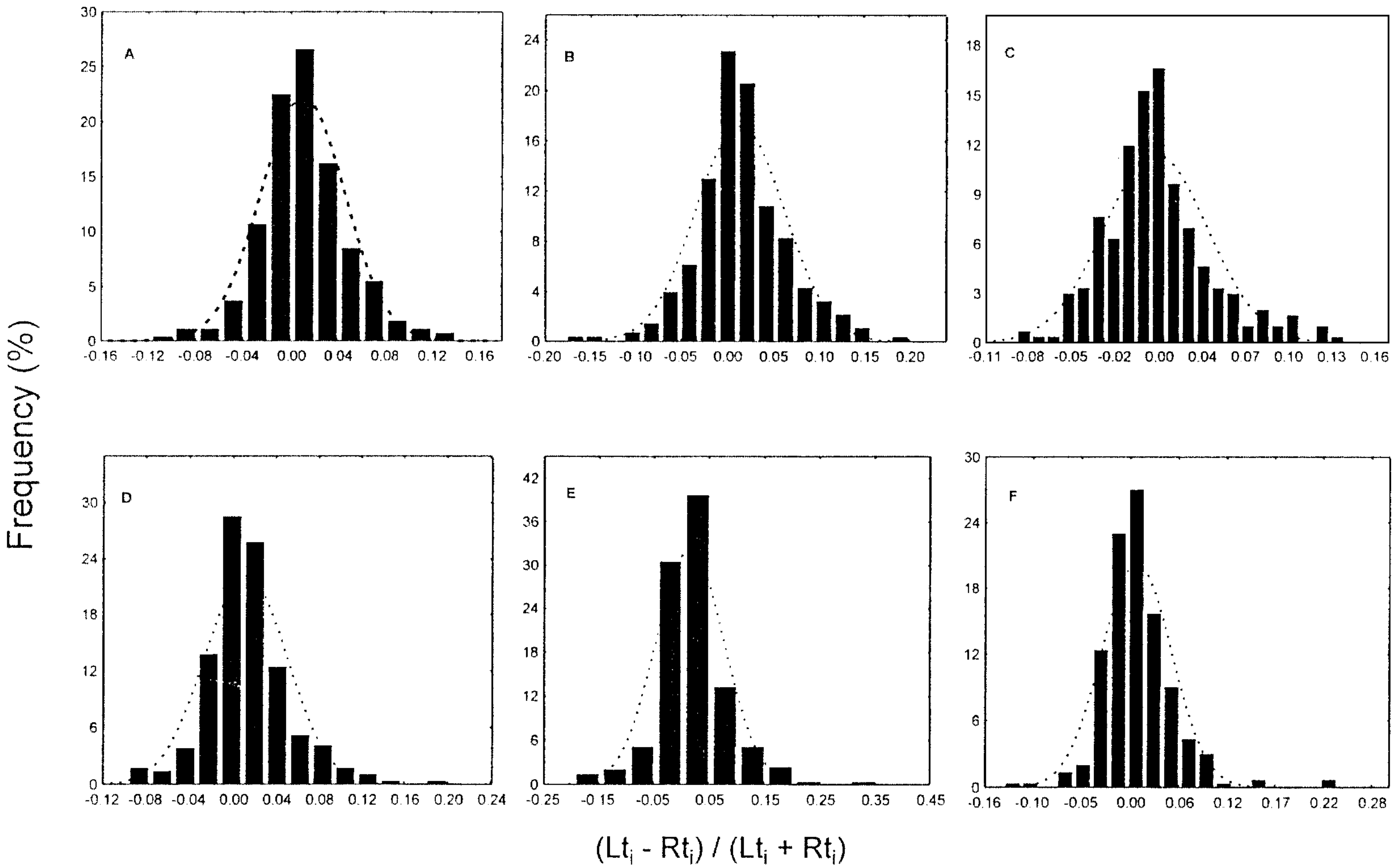

Fig. 2. Distribution of Lt-Rt differences of selected traits to illustrate lack of antisymmetry in studied traits. **A:** Second ray. Kolmogorov-Smirnov d = 0.055, $P > 0.05$. **B:** Metacarpal 2 bone. Kolmogorov-Smirnov d = 0.083, $P > 0.05$. **C:** Proximal phalanx 2. Kolmogorov-Smirnov d = 0.085, $P > 0.05$. **D:** Third ray. Kolmogorov-Smirnov d = 0.078, $P > 0.05$. **E:** Metacarpal 3 bone. Kolmogorov-Smirnov d = 0.073, $P > 0.05$. **F:** Proximal phalanx 3. Kolmogorov-Smirnov d = 0.084, $P < 0.05$. Deviation from normality assumption is due to kurtosis: 6.82 ± 0.28.

TABLE 1. Kruskal-Wallis and parametric ANOVA of FA in simple traits (group 1) as compared with FA in complex traits (group 2) by hand bones ray

Variable	Group	N	Mean rank	χ^2	*P*	V	F	*P*
I-RAY2	1	245	343.7	267.4	<0.001	0.3631	2.80	<0.001
	2	245	147.3			0.1296		
I-RAY3	1	271	371.8	241.8	<0.001	0.2991	2.07	<0.001
	2	271	171.2			0.1441		
I-RAY4	1	254	352.4	263.7	<0.001	0.3015	2.09	<0.001
	2	254	156.5			0.1444		
I-RAY5	1	199	281.3	235.3	<0.001	0.4400	2.27	<0.001
	2	199	117.7			0.1936		

Spearman rank order correlation. Here *i* refers to individual and *j* to a specific trait. Principal component analysis and multidimensional scaling were then performed on the respective matrices of correlations to identify related and unrelated arrays of FAs in a matrix including 2,774 elements.

Since a large number of traits (72 bone measurements + 4 rays) with low correlations may inflate eigenvalues, only factor scores equal to or higher than 0.30 were retained.

RESULTS

Comparison of FA in complex and simple traits

In this part of the study, our working hypothesis was that complex traits possess lower FA as compared with simple traits, or alternatively the null hypothesis that no differences in FA exist between these two categories of traits.

Table 1 provides the results of comparison of both FA measures for each ray and corresponding individual bones that made up the complex trait. As can be attested by the Kruskal-Wallis test, FA2 measures were much lower in complex traits. Table 1 shows that the mean ranks for simple traits varied between 281.3 and 371.8 vs. 117.7 and 171.2 in complex traits. The obtained χ^2 values indicated that differences were all highly significant ($P < 0.001$). Comparison of FA6 measures, using F-tests, showed virtually the same results (Table 1). Figure 3 demonstrates the mean + standard deviation for FA2 in both categories of traits according to ray. Again, vast differences are obvious.

These results raise two questions. The first is whether it is possible that the decrease of FA in complex traits is a result of compensation. That is, the random fluctuation in the size of different bones within the ray is randomly directed, and therefore the differences cancel Rt-Lt in the total ray length. The second is whether the FA of each simple trait is consistently higher than the FA of the corresponding ray.

To examine these two questions, we first performed a simulation of the FA6 of complex traits by random combinations of paired bones from different individuals. Our working hypothesis here was that randomly adding together different elements to create a new ray will significantly increase the FA of the complex trait. New rays and their respective FA6 were created 300 times, and the distribution of the corresponding pseudo-FA6 values were compared with the real one. Secondly, we compared the FA of each individual bone separately with the respective ray's FA.

The comparison of the observed FA6 values with 300 simulated distributions of each of the studied complex traits showed that in all instances the observed variance was significantly higher than those simulated randomly (Table 2). In fact, the observed variance was larger than the highest simulated value. Such a result was in complete contradiction to our expectation. However, it can be expected if a slight correlation exists between the Rt-Lt differences of the bones composing the same ray. For example, consider the extent of complex trait asymmetry, for the sake of simplicity, composed of two simple traits, *X* and *Y*. It can be defined as follows:

$$FA_{(x+y)} = FA_{(x)} + FA_{(y)} = \frac{2(X_L - X_R)}{(X_L + X_R)} + \frac{2(Y_L - Y_R)}{(Y_L + Y_R)}. \quad (1)$$

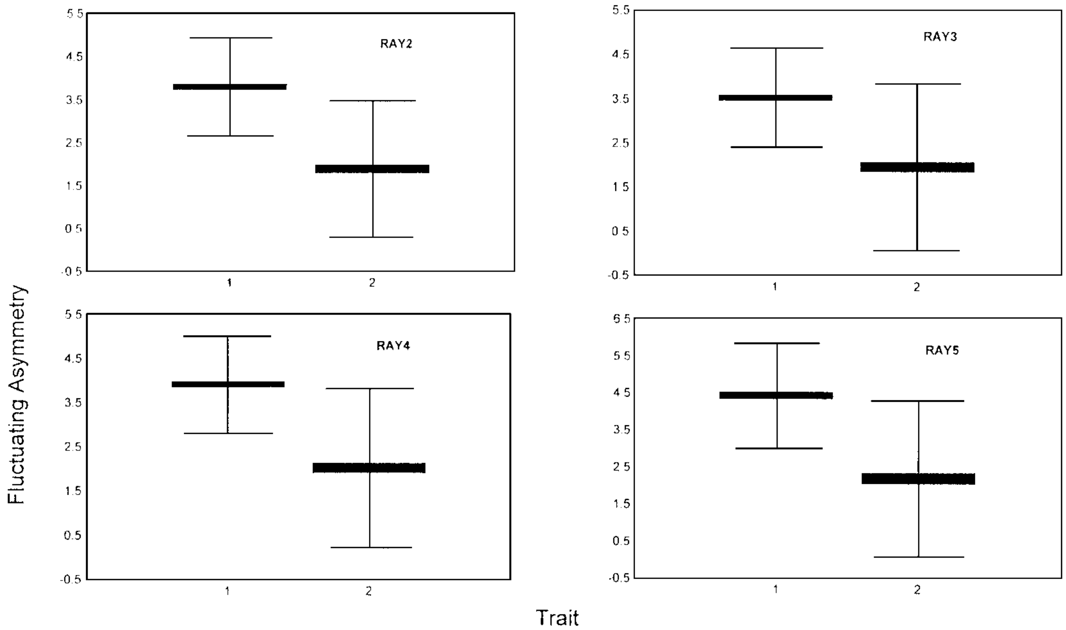

Fig. 3. Mean fluctuating asymmetry (FA2) in simple traits (1) and complex trait (2) according to ray.

TABLE 2. Comparison of observed distribution of FA6 values in complex traits with 300 simulated distributions

Variable	Observed FA6	Simulated estimates of FA6			
		Mean	Minimum	Maximum	*P*
FA6-RAY2	2.65	1.42	0.95	2.12	0.003
FA6-RAY3	3.60	1.96	1.14	3.24	0.003
FA6-RAY4	3.48	1.87	0.97	3.19	0.003
FA6-RAY5	5.38	2.54	1.33	4.74	0.003

TABLE 3. Matrix of Pearson correlations between the simple traits Lt-Rt differences within their respective rays

	Metacarpal	Proximal	Middle
RAY2			
Proximal	0.4288***		
Middle	0.2666***	0.3009***	
Distal	0.2941***	0.2167***	0.3682***
RAY3			
Proximal	0.3410***		
Middle	0.3027***	0.1542**	
Distal	0.2652***	0.1707**	0.2713***
RAY4			
Proximal	0.4267***		
Middle	0.3066***	0.3601***	
Distal	0.2674***	0.1193*	0.2187***
RAY5			
Proximal	0.2336***		
Middle	0.4234***	0.2612***	
Distal	0.2873***	0.1480*	0.3497***

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

If there is no correlation between $FA_{(x)}$ and $FA_{(y)}$. If, for example, a linear relationship does exist between $FA_{(x)}$ and $FA_{(y)}$, then it can be easily expressed as a linear regression equation—that is, $FA_{(y)} = a + b\, FA_{(x)} = a + 2(X_L - X_R)/(X_L + X_R)$, or, for simplicity's sake, $a + b(X_L - X_R)/\bar{X}$. It follows then that, if b = 0,

$$FA_{(x+y)} = (X_L - X_R)/\bar{X} + a$$

or, if b > 0, (2)

$$FA_{(x+y)} = (X_L - X_R)/\bar{X} + a + b(X_L - X_R)/\bar{X}.$$

This means that if the correlation between the simple trait asymmetries is positive, then the complex trait's FA will be higher than the one expected under no correlation. Under no correlation, if $X = Y$, both mean Rt-Lt difference and its variance (i.e., FA6) will tend to be zero due to a random direction of differences between the different pairs of bones composing the ray.

We therefore tested pairwise correlations between the respective four bone asymmetries within each ray (Table 3). Our expectation was now confirmed: all correlations

TABLE 4. Comparison of FA6 in simple traits with FA6 of corresponding complex trait by RAY [1]

Variable	FA6	F-test vs. I-RAY
RAY2	0.130	—
Metacarpal	0.240	1.85**
Proximal	0.130	1.00 (NS)
Middle	0.360	2.78***
Distal	0.722	5.57***
RAY3	0.144	—
Metacarpal	0.384	2.66***
Proximal	0.192	1.05 (NS)
Middle	0.185	1.28*
Distal	0.221	1.53**
RAY4	0.144	—
Metacarpal	0.397	2.75***
Proximal	0.137	0.95 (NS)
Middle	0.168	1.16 (NS)
Distal	0.504	3.49***
RAY5	0.194	—
Metacarpal	0.436	2.25***
Proximal	0.122	0.64****
Middle	0.578	2.98***
Distal	0.624	3.22***

[1] NS, not significant.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
**** $P < 0.01$, opposite order of traits comparison.

TABLE 5. Comparison of FA2 in simple traits with FA2 of corresponding complex trait by RAY [1]

Variable	N	Mean rank	χ^2
RAY2			
Metacarpal	271	234.2	27.5***
	271	308.8	
Proximal	271	274.4	0.1 (NS)
	271	268.6	
Middle	271	223.9	39.3***
	271	319.1	
Distal	271	199.3	108.1***
	271	343.7	
RAY3			
Metacarpal	291	230.7	62.0***
	291	352.3	
Proximal	291	290.2	0.2 (NS)
	291	292.8	
Middle	291	281.1	1.5 (NS)
	291	301.9	
Distal	291	222.4	84.7***
	291	360.6	
RAY4			
Metacarpal	283	234.7	49.9***
	283	332.3	
Proximal	283	300.9	9.2****
	283	266.1	
Middle	283	277.1	0.3 (NS)
	283	289.9	
Distal	283	224.1	77.9***
	283	342.9	
RAY5			
Metacarpal	275	223.2	40.9***
	275	327.8	
Proximal	275	304.3	12.2****
	275	246.7	
Middle	275	217.5	47.7***
	275	333.5	
Distal	275	213.7	62.9***
	275	337.3	

[1] NS, not significant.
*** $P < 0.001$.
**** $P < 0.01$, opposite order of traits comparison.

within the ray were positive, and the majority were also statistically significant. Hence, when we performed simulation, full randomization of bone sequences within each ray was achieved, and thus FA6 decreased.

Table 4 gives the results of the comparison of the FA6 measure in complex traits against each of the respective simple traits. Of interest is the fact that although three out of four comparisons within every ray confirms our working hypothesis ($P < 0.05$ or smaller), the FA6 of the proximal phalanx consistently contradicted it. In three instances the difference was not significant, and RAY5-FA6 was even significantly higher.

Table 5 provides the result of a similar comparison of the FA2 measure. The results generally are in agreement with FA6 comparisons. However, the statistically significantly higher RAY-FA2 was observed in two instances, namely, RAY4 and RAY5 vs. corresponding proximal phalanx FA2. In two other comparisons, RAY3-FA and RAY4-FA vs. respective middle phalanges FA, the differences were not significant, although the FA of simple traits tended to be numerically higher as expected.

Thus, the low FA of the rays considered in this study is hardly an inherent feature of the complex traits but rather shows that it is indeed a result of a compensation due to a random direction of small fluctuations in the size of the simple traits.

Relationship between variability of trait and FA

Table 6 shows Pearson correlation coefficients between average FA2 value and CV for 72 studied traits according to sex and in three age cohorts. As seen, all the correlations were positive and statistically highly significant, ranging between 0.739 in young females and 0.897 in young males. The χ^2 test for correlation coefficients heterogeneity (Sokal and Rohlf, 1981) showed no significant differences among age cohorts according to sex. Thus the respective correlations in total groups varied between 0.878 and

TABLE 6. Relationship between FA and CV in all studied traits

Age/sex	N	r	*P*
Males			
<30	61	0.897	<0.001
30–60	57	0.886	<0.001
>60	61	0.868	<0.001
Total[1]	179	0.966	<0.001
Females			
<30	17	0.739	<0.001
30–60	29	0.828	<0.001
>60	78	0.869	<0.001
Total[2]	124	0.878	<0.001
Grand total	303	0.893	<0.001

[1] $\chi^2 = 0.58$; D.F. = 2; $P > 0.5$.
[2] $\chi^2 = 5.12$; D.F. = 2; $P > 0.5$.

0.966. All correlations were highly significant statistically ($P < 0.001$) and, as seen in Figure 4, did not substantially deviate from the linear correlations. When a few traits that possessed very low FA (at the bottom of each figure) are excluded, the linearity is almost perfect.

Estimation of hand-wide FA

To examine the extent to which different measures of FA correspond one to another, we computed the matrix of pairwise correlations between individual FA2 estimates. Table 7 shows results of a principal component analysis performed on the Pearson correlation matrix. Since many correlations were weak and statistically not significant on the one hand, but the number of studied traits was large (76), (including 4 rays) on the other hand, factor scores lower than 0.30 were neglected. Under this condition, by eigenvalue one criterion, seven principal components were extracted. They collectively explained only 17.7% of the total variation, with principal component 1 (PC1) responsible for 6.11% of the variance. This finding shows that in general there is quite a low correspondence in FA2 between different traits. A few groups, each with a small number of traits, can nevertheless be indicated. Of these, the most interesting perhaps is PC1, which retained four rays and four metacarpal bone lengths. Note here, however, that the FA of bone lengths within each ray showed positive correlation one with the other (Table 3).

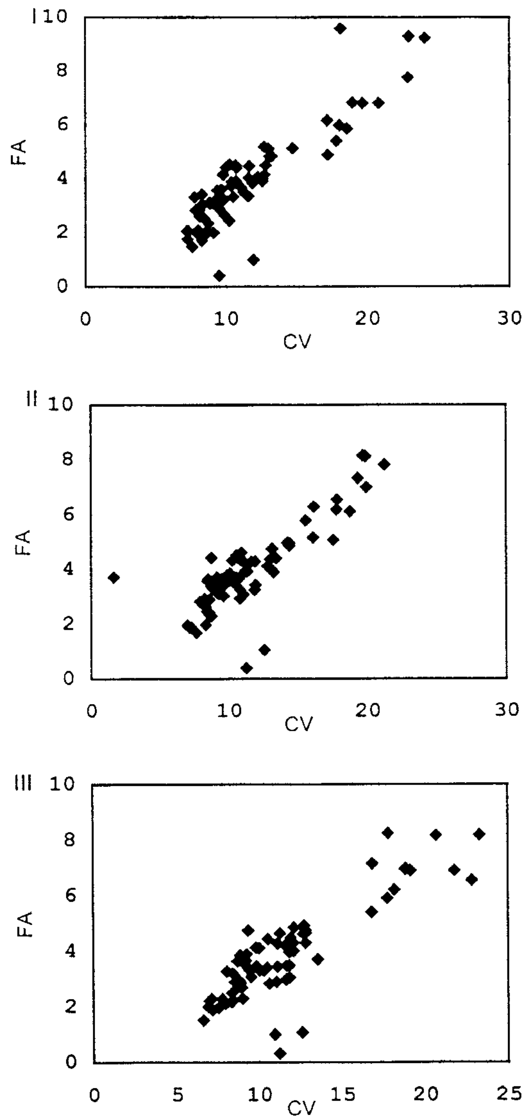

Fig. 4. Relationship between population mean FA2 and CV in studied traits according to age cohort.

PC2 united FA2 measures of proximal phalanges, and PC3 is the factor of second ray on bone width asymmetry. Other principal components were loaded with different combinations of various bones and their measurements. Thus, in general there is a relatively low integration among various FA measures of hand bones, and yet among some sets very substantial correlations can exist.

TABLE 7. Principal component analysis of FA measurements

	FCT-1	FCT-2	FCT-3	FCT-4	FCT-5	FCT-6	FCT-7
1 FA-IRAY2	0.73084	0.35023					
2 FA-IRAY3	0.72874	0.43388					
3 FA-IRAY4	0.84509						
4 FA-IRAY5	0.70142						
5 A2MLEN	0.68271						
6 A3MLEN	0.75155						
7 A4MLEN	0.82895						
8 A5MLEN	0.76489						
9 A3MWID							0.48701
10 A5MWID					0.66048		
11 A5MCAN					0.74445		
12 A2PLEN		0.60031					
13 A2PWID					0.39904		
14 A3PLEN		0.83827					
15 A4PLEN		0.6502				0.41027	
16 A4PWID			0.36933		0.3221		
17 A4PCAN						0.75335	
18 A5PCAN				0.66719			
19 A5PPWIDE							0.32893
20 A2SLEN		0.48995					
21 A2SWID			0.57141			0.33032	
22 A2SPWIDE			0.32963				
23 A2SDWIDE			0.56342				
24 A3SLEN	0.31181						0.57773
25 A3SCAN				0.39722			
26 A3SPWIDE	0.31978						
27 A4SWID					0.34768		
28 A4SCAN						0.41111	
29 A5SPWIDE						0.53351	
30 A5SDWIDE				0.71698			
31 A2DLEN							0.77054
32 A2DBAS			0.78066				
33 A3DWID				0.42898			
34 A5DWID				0.45334			
Eigenval	4.77	2.04	1.51	1.49	1.37	1.30	1.27
V%	6.11	2.62	1.92	1.91	1.76	1.67	1.63

The inspection of the matrix of Spearman rank order correlations and the corresponding results of multidimensional scaling were in agreement with these results, although the magnitude of the majority of correlations was even lower.

DISCUSSION

While the majority of previous studies mostly asked questions concerning the differences in FA among individuals who may have varied in their health status, in phenotypical characteristics, and in heterozygosity level or who were exposed or not exposed to genetic or environmental stresses (Parsons, 1990, 1994; Livshits and Kobyliansky, 1991; Fraser, 1994; Mitton, 1994, 1995; Livshits and Smouse, 1993, 1994; Moller, 1996), the present study focused on differences in FA among the different traits of the same organ, namely the hand skeleton.

The results we obtained clearly confirm the hypothesis that positive correlation is expected between the two expressions of developmental instability of traits (i.e., between CV and FA). Our results on 72 measurements of FA2 were consistent among age cohorts and between the two sexes. The correlations were high in all instances and highly significant. On the other hand, no substantial correlation was observed between measurement error and either FA2 or CV. That is, the less a trait is developmentally stable (or more variable) in terms of interindividual variation, the higher the FA it possessed. However, it is not obvious from this relationship whether more variable traits are more prone to changes due to genetic mutations or environmental insults. The answer to this question may contribute important knowledge and clarification to the problem of the relationship between FA and

health deviations (Livshits and Kobyliansky, 1991; see array of papers, in particular proceedings of the discussions moderated by Kaufman, Session 2, and by Fraser, Session 3, edited by Markow, 1994; Fraser, 1994; Naugler and Ludman, 1996a; Moller, 1996; Kobyliansky et al., 1997a; Thornhill and Moller, 1997).

Our results also agree with the assumption that for developmentally homogeneous traits the more complex traits possess higher stability (lower CV and FA) than the corresponding simple traits (Soule, 1982). However, this may be due to the fact that the complexity of traits may have a similar effect on CV and FA. Indeed, $CV_{(T)} = SD_{(T)}/M_{(T)}$, where $SD_{(T)}$ and $M_{(T)}$ are the standard deviation of a total length of a complex trait (e.g., ray) and its corresponding mean value. $M_{(T)}$ does not depend on the correlation between the respective simple traits (e.g., X and Y). However, $SD_{(T)}$ does—that is, $V_{(T)} = V_{(X)} + V_{(Y)} + 2COV_{(XY)}$. Thus, the higher the correlation, the higher the corresponding $V_{(T)}$ and hence larger $CV_{(T)}$. At the same time, as we showed in formulas 2 and 3, the correlation between X and Y will increase $FA_{(T)}$ on $b(X_L - X_R)/X$ value, or, to make this formula comparable with the $V_{(T)}$ formula, we can define $X_L - X_R$ and $Y_L - Y_R$ differences by dX and dY, respectively. Then, $FA_{(T)} = dX + a + COV_{(dXdY)}dX/V_{(dx)}\overline{X}$.

Obviously, if $r > 0$, FA_T will be higher than the one expected under no correlation. The additional corollary of this relationship is the expectation that, on average, the FA of a complex trait will be lower than of the simple one, which was indeed confirmed in the data (Tables 2, 3). However, as seen in Tables 5 and 6, it is not necessarily a consistent result. Some simple traits may have FA2 values lower than the corresponding complex characters. Yet, under no correlation between simple traits, the probability of $dX_i > 0$ is equal to the probability of $dY_i < 0$ (i.e., their additive effect will lead FA_T to zero value if the magnitude of $FA_X = FA_Y$).

The existence of correlations between FA measures of different traits still remains an open question. As mentioned in the introduction, while some authors believe that FA may be an organism-wide property (e.g., Leamy, 1994), others assume that it reflects only trait-specific homeostasis (Soule and Cuzin-Roudy, 1982). The results of different studies are quite contradictory. Some studies found no or very little concordance among estimates of FA based on different bilateral structures (Livshits et al., 1988; Brakefield and Breuker, 1996; Evans and Marshall, 1996). However, others showed in a variety of species that the results are actually ambiguous (Leamy, 1994; Dufour and Weatherhead, 1996) since some correlations are significant and some are not. In Leamy's (1994) study, significant correlations were found mostly between developmentally closely related traits. However, they were very different when estimated within and between populations. In the present study, the majority of correlations were also low and not significant, though developmentally the majority of considered traits are related closely. It seems that significant correlations appeared mostly between traits that were related not only developmentally but also functionally and that participate actively in the function performance. For example, the highest correlations were observed between the FA of the lengths of rays and the lengths of the phalanges, namely between bones involved in synergetic action—for instance, grasping. Those were independent of the FA of the phalangeal widths, while the latter correlated one with another in many instances. And yet the source of this covariation, if this is not hidden DA, is still not clear. Much remains to be learned in future investigations.

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